# Thermal Influences on the Activity and Energetics of Yellow-bellied Marmots (*Marmota flaviventris*)

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**Abstract**

*The thermal environment of microhabitats used by yellow-bellied marmots (*Marmota flaviventris*) at three study sites in the Elk Mountains of southwestern Colorado was characterized using the standard operative temperature ($T_{es}$) method. Marmots typically used only two aboveground microhabitats—meadows, where they foraged, and rocks near the burrow, where they often sat. The $T_{es}$'s calculated for foraging areas were often below 0° C before 0800 hours and often exceeded the upper limit of marmots' thermoneutral zone from late morning to midafternoon on clear days. Higher wind speeds over rocks produced $T_{es}$'s up to 10° C less than in foraging areas. Marmots responded to stressfully high $T_{es}$'s by reducing aboveground activity, reducing the length of foraging bouts, and tolerating transient increases in body temperature. Foraging activity during midday hours was greater on cloudy days and at a high elevation site with lower average $T_{es}$'s. Young responded to stressfully low $T_{es}$'s by timing daily activity to avoid the lowest $T_{es}$'s. Although marmots generally avoided foraging at the most stressful $T_{es}$'s, they sometimes foraged at stressful $T_{es}$'s, presumably when that option was necessary to meet daily energy demands and preferable to the alternative of forgoing foraging. Under most conditions, stressful $T_{es}$'s did not appear to limit time needed for foraging, but thermal constraints may have been important for young that also faced declining food quality at the end of the growing season.*

## Introduction

Animals must allocate time and energy among many competing demands. Patterns of allocation are often interpreted within a framework of optimality theory, assuming that observed patterns reflect selection for optimal alloca-

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tion among maintenance, growth, reproduction, and other activities (e.g., Krebs and McCleery 1984). While such an approach is a useful heuristic for the study of time and energy allocation, knowledge of proximate environmental factors that influence activity is equally important to understanding observed patterns. Thermal constraints limit the activity of animals ranging from ectothermic invertebrates to endothermic vertebrates (e.g., Heller and Gates 1971; Chappell and Bartholomew 1981*b*; Christian, Tracy, and Porter 1983; Kingsolver 1983; Bennett et al. 1984; Goldstein 1984; Grant and Dunham 1988) and can influence allocation by restricting time available to acquire resources in thermally intolerable microhabitats or by adding thermoregulatory costs to the energetic costs of activity. By quantifying thermal conditions in comparative terms and predicting animals' responses to different conditions, biophysical modeling techniques (Porter and Gates 1969; Morhardt and Gates 1974; Bakken 1976, 1980, 1981; Robinson, Campbell, and King 1976; Mahoney and King 1977; Gates 1980) may permit integration of proximate environmental influences with theories of time and energy allocation to improve understanding of observed patterns of allocation.

This study used biophysical modeling methods to investigate thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*), large hibernating ground squirrels that typically inhabit montane areas with short growing seasons. In the Elk Mountains of southwestern Colorado, marmots have only 4–5 mo to reproduce, grow, and deposit fat for hibernation. Young must attain a threshold weight to survive hibernation, and reproductive success of females may depend partly on fat reserves remaining after hibernation (Andersen, Armitage, and Hoffman 1976; Armitage, Downhower, and Svendsen 1976). Factors influencing the allocation of energy to growth and fat deposition are thus of particular importance. Foraging is presumably a high-priority activity during the marmots' short active season, yet marmots spend much time in their burrows from late morning to midafternoon; Travis and Armitage (1973) suggested that heat stress limits midday activity. This study evaluated the importance of thermal constraints on foraging, as well as the variation of thermal influences on activity among age groups and among marmot colonies at different elevations.

## Material and Methods

### *Study Sites*

Marmots were studied at three sites in the Elk Mountains of Gunnison County, Colorado: Marmot Meadow (MM) during the summers of 1981–

1984, Picnic (PIC) during the summer of 1983, and North Pole Basin (NPB) during the summers of 1983–1984. Located on opposite sides of the East River at an elevation of 2,900 m, MM and PIC include talus slopes where the marmots maintained home burrows, an area of open meadow, and are bordered in part by forest (detailed description in Armitage 1974). At NPB, a 3-km-long hanging valley at an elevation of 3,400 m, 10 km northwest of MM and PIC, burrows were located on the valley floor within rock outcrops bordered by patches of open meadow and willow thicket (detailed description in Andersen et al. 1976).

*Body Temperature and Behavioral Observations*

Body temperature ($T_b$) of 13 animals studied in 1983 and seven animals studied in 1984 was monitored with either Telonics IMP/200/L or Mini-Mitter model L temperature-sensitive telemetry transmitters (Melcher 1987). Telonics transmitters measured 5.8 × 2.0 cm and weighed 22–27 g when encased in a mixture of paraffin/elvax. Mini-Mitter model L's measured 1.8 × 4.4 cm and weighed 17 g. Transmitters were individually calibrated in a water bath from 30°–45°C; bath temperature was read to the nearest 0.1°C with a Bailey BAT-12 thermocouple thermometer previously calibrated against a Taylor Instruments mercury thermometer having a systematic error of 0.01°C. Transmitter pulse rate was linearly related to temperature over the calibration range.

Transmitters were implanted intraperitoneally in animals anesthetized with Ketaset (ketamine hydrochloride, 1.0 mg/mL) at a dosage of 1 mL/kg diluted 1:1 with sterile physiological saline. Animals were generally released the day following surgery and behaved normally upon release. Recapture of animals revealed no rupture of the incision, animals always appeared healthy, and healing occurred within 1 wk. In 1983 and June 1984 transmitters were implanted several days to several weeks before initiating studies; in September 1984 transmitters were implanted within 24 h of beginning studies.

Animals were observed from tree platforms (MM and PIC) or from behind natural blinds of willow (NPB) using 8 × 24 binoculars. Telonics transmitter signals were received with a Telonics TR-1-20 receiver and a hand-held directional antenna. A Telonics TDP-2 digital data processor was used to convert pulse rate to interpulse interval (in milliseconds); interpulse intervals were recorded manually and later converted to $T_b$ using the calibration regression for each transmitter. When signals were occasionally too weak for the decoder, 30 pulses were timed to the nearest 0.01 s instead. Signals from Mini-Mitter transmitters were received with a Mini-Mitter CH-6 receiver.

Thirty pulses were timed to the nearest 0.01 s and converted to $T_b$. The $T_b$ was recorded every 15 min during observation sessions, occasionally more frequently when an animal changed activity state. Location (burrow, rock, grass, or woods) and activity (sit, forage, or locomote) were censused at 20-min intervals during 1981 and were recorded continuously for those animals whose location was known during the remaining studies. During data analysis, locomotion associated with foraging was added to foraging time, and miscellaneous behaviors such as grooming, greeting, and play were pooled with sitting.

*Microclimate Measurements*

Microclimate data were recorded concurrently with behavior and $T_b$ (Melcher 1987) except during 1981 when equipment was available to concurrently record only solar radiation ($Q_{sol}$); other variables were measured on days when animals were not being observed. Solar radiation was measured with a Licor LI-200S pyranometer sensitive to wavelengths between 100 and 1200 nm. Net radiation was measured with a miniature Fritschen-type net radiometer. Air temperature ($T_a$) at 10 cm and soil temperatures were measured with thermistor probes. Air temperature probes were shielded with 15 × 9-cm sections of PVC tubing painted flat white. Wind speed was measured between 0.5 and 1.0 m with Rimco miniature cup anemometers. Wind speed at marmot height was calculated later from wind profiles measured at the same sites. Output from microclimate sensors was fed into a Campbell CR-21 micrologger that averaged output every 15 min and stored the averaged values on cassette tape. Microclimate data were later decoded from cassette tape with a Campbell A235 interface and a decoding program.

*Modeling of Thermal Energy Exchange*

We modeled thermal energy exchange using standard operative temperature ($T_{es}$) (Bakken 1976, 1980, 1981) to describe the thermal environments experienced by marmots. $T_{es}$ is an index used to establish thermal equivalence between laboratory and outdoor environments (Bakken 1980) and specifies the temperature of a laboratory enclosure with standard convection conditions that would yield the same net heat flow experienced by an animal in its natural environment (Bakken 1981). Thus an animal's metabolic response to a given $T_{es}$ can be equated with its response in a metabolic chamber at a $T_a$ the same as $T_{es}$. The theory, development, and application of the $T_{es}$ approach are discussed in detail by Bakken (1976, 1980, 1981).

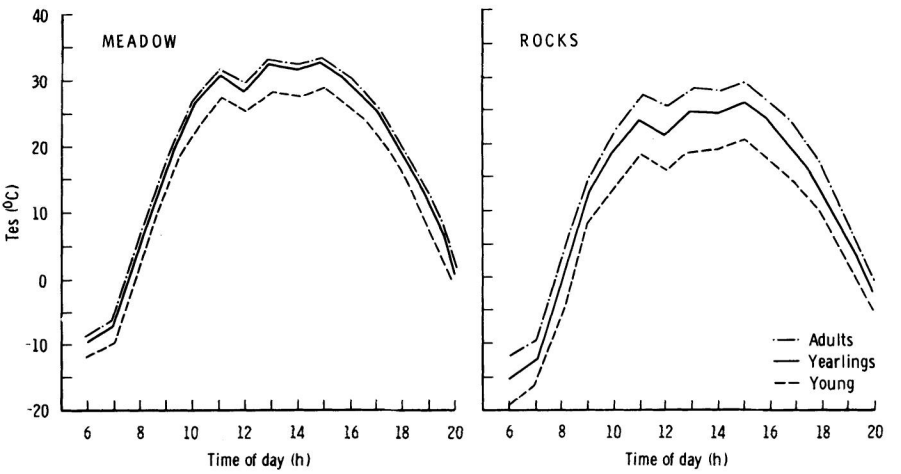


*Fig. 1.* $T_{es}$*'s for adult, yearling, and young marmots in the two most frequently used aboveground microhabitats, meadow and rocks near the burrow. Values are calculated hourly averages from a week-long study at Marmot Meadow during mostly clear weather in July.*

The value $T_{es}$ is defined as follows:

$$T_{es} = T_b - [(r_{es} + r_{bs})/(r_e + r_b)](T_b - T_e),$$

where $r_e$ is the thermal resistance between outer surface and environment (s $m^{-1}$), $r_{es}$ is the value of $r_e$ under standard conditions (s $m^{-1}$), $r_b$ is body resistance (s $m^{-1}$), $r_{bs}$ is the value of $r_b$ under standard conditions (s $m^{-1}$), and $T_e$ is operative temperature. These variables follow Bakken (1981) and Mahoney and King (1977). The value $T_e$ is defined as follows:

$$T_e = T_a + (r_e/c_p)R_{ni},$$

where $c_p$ is the specific heat of air (1.01 kJ $kg^{-1}$ $K^{-1}$) and $R_{ni}$ is the net absorbed solar and thermal radiation (W $m^{-2}$). It was calculated from measured microclimate conditions and animal characteristics following the procedure outlined in Mahoney and King (1977). We calculated $r_{es}$ for both standard conditions (marmots in metabolic chambers) and field conditions using heat-transfer theory. We estimated $r_{bs}$ from measurements of oxygen consumption and evaporative water loss (Kilgore and Armitage 1978; Ward 1980; Melcher 1987) using equation (4) in Robinson et al. (1976). The effects of convection on heat transfer between animals and the environment, particularly under conditions of high $Q_{sol}$, are complex (Walsberg, Campbell, and King 1978) but important: $T_{es}$'s calculated by Chappell and Bartho-

lomew (1981*a*) for the antelope ground squirrel differed from $T_e$'s (an index of the potential driving heat flow, exclusive of changes in thermal resistance related to convection) by 5°–10°C under certain conditions. Wind-speed dependence of $r_b$ is known for few species and was not measured for marmots, but instead was estimated with values for the white rabbit (Monteith 1973). Admittedly, this is less satisfactory than having actual values for marmots, but, since wind speed varied during studies and among sites, and since the adjustment for $r_b$ amounted at most to only 10%–20% of total $r_b$, this approximation was chosen over the alternative of calculating only $T_e$. We followed the procedure outlined in Buttemer et al. (1986), initially assigning $r_b$ for a given field $T_e$, then adjusting for wind-speed effects. Because an animal varies its thermal resistance in response to $T_{es}$, rather than to $T_a$ or $T_e$, the equation for $T_{es}$ could not be solved directly (Chappell and Bartholomew 1981*a*) and hence was solved numerically.

## Results

*Standard Operative Temperature*

*Microhabitat.* Aboveground microhabitats available to marmots included rocks near the burrow, open meadow, willow stands, and woods. Only two of these, rocks and open meadow, were used frequently. Neither area offered much shade; differences in microclimate between them depended mainly on differences in wind speed. Higher wind speeds over the top of rocks 0.5–1.0 m above the surrounding vegetation produced $T_{es}$'s for adults up to 5°C lower than in the meadow, and up to 10°C lower for young (fig. 1).

*Age Class.* The $T_{es}$'s for young were 3°–10°C lower than those for adults in the same microhabitat (fig. 1). The $T_{es}$'s for yearlings were lower than the $T_{es}$'s for adults but higher than those for young. The magnitude of differences among $T_{es}$'s calculated for the three age classes varied between the two main aboveground microhabitats used by marmots—meadow and rocks near the burrow (fig. 1). Higher wind speeds characteristic of conditions at rocks where marmots often sat accentuated differences in $T_{es}$ among age classes.

*Season and Weather.* Marmot Meadow was the only site sampled during all months from June through September; results in this section refer to that site. On sunny days throughout the season, $T_{es}$ rose rapidly after sunrise, remained high until late afternoon, then fell rapidly after sunset (fig. 1).

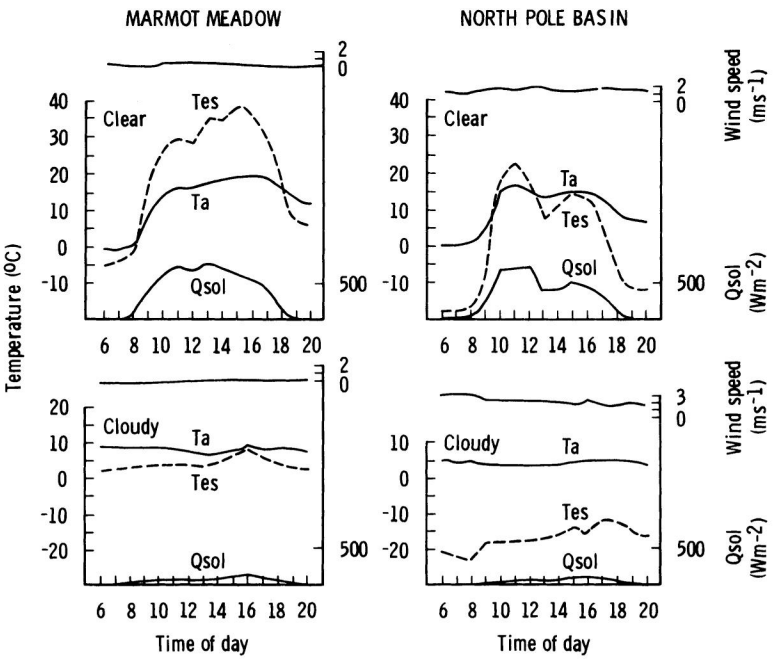


*Fig. 2. Measured microclimate conditions and calculated* $T_{es}$*'s for young on a clear (top) and cloudy (bottom) day at Marmot Meadow and North Pole Basin in September.*

Daily range of $T_{es}$ was quite consistent for much of the season. The $T_{es}$'s for adults typically rose from lows near −8°C at 0600 hours to highs of 31°–33°C between 1300 and 1500. The daily range of $T_{es}$ was greatest on clear days in September; $T_{es}$ for adults exceeded 40°C by midafternoon. Wind velocity near the ground was greatly attenuated by increased vegetation height in September, hence the higher midafternoon $T_{es}$'s. The $T_{es}$'s on cloudy days rose and fell in a pattern similar to those on clear days, but the range of $T_{es}$ was much smaller, from lows near 2°C to highs near 25°C. On a heavily overcast September day, $T_{es}$ rose from a low of 3°C to a high of only 9°C.

*Study Site.* The $T_{es}$'s at NPB usually were considerably lower than the $T_{es}$'s calculated from concurrently measured microclimate conditions at MM (fig. 2). The $T_a$'s at NPB usually averaged lower than those at MM, more frequent late afternoon clouds reduced direct solar radiation, and wind speeds were consistently higher. The $T_{es}$'s calculated for young at MM on a clear September day ranged from −5.1°C at 0600 hours to 38.9°C at 1500; the comparable values for NPB were −17.6° and 22.7°C. On a heavily overcast September

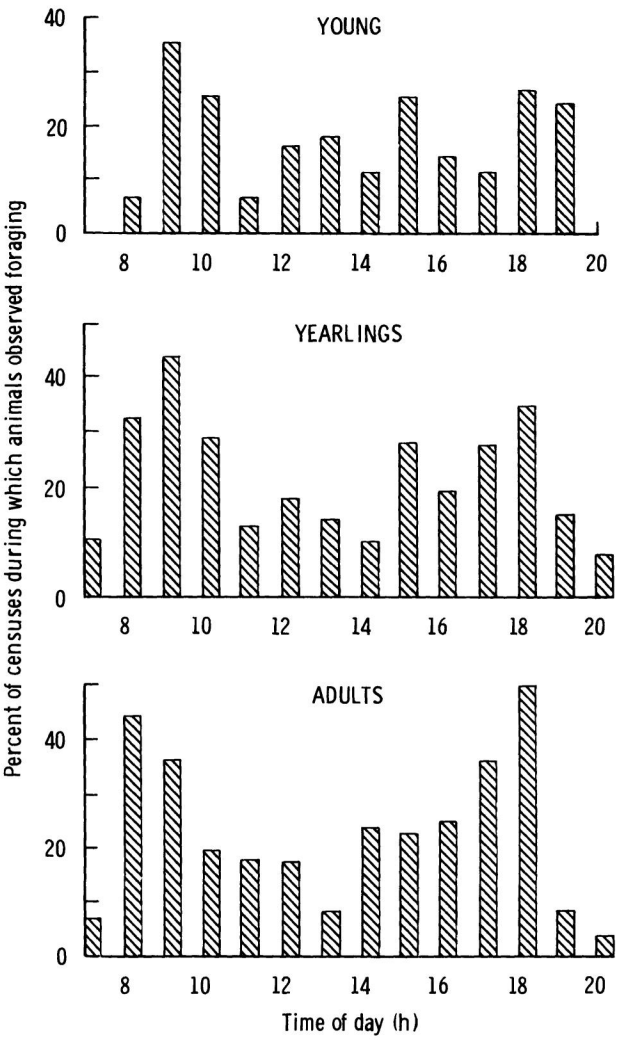


*Fig. 3. Foraging activity of different age classes at Marmot Meadow during 5 d of observation in July 1981. Activity was censused at 20-min intervals; values presented are the average number of censuses during which an animal was observed foraging during each hourly interval, averaged for all members of a given age class. Number of animals in each age class varied among days, ranging from 2 to 4 adults, 6 to 7 yearlings, and 7 to 18 young. Equipment to record microclimate conditions simultaneously with behavior was limited to a solar radiometer in 1981; hence, no* $T_{es}$*'s were calculated. Weather was similar to July weather in 1983, and the consistency of the daily cycle of* $T_{es}$*'s during July 1983 suggests that* $T_{es}$*'s for July 1981 were similar.*

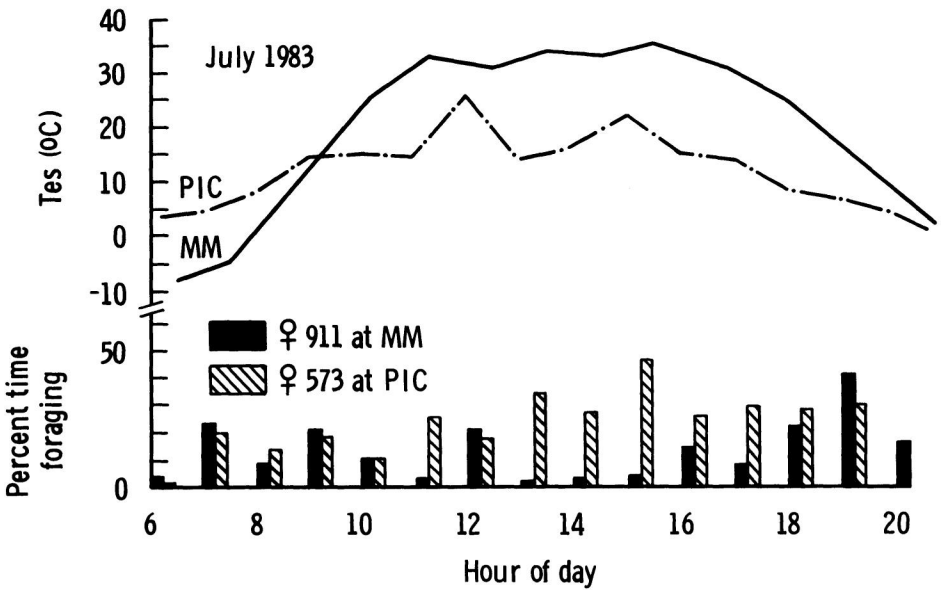


*Fig. 4. Foraging activity (percentage of time spent foraging) and* $T_{es}$*'s averaged over hourly intervals for adult female 911 during a mostly clear week at Marmot Meadow and for female 573 during a mostly cloudy week at Picnic during July.*

day $T_{es}$'s for young at MM ranged from 1.3° to 8.3°C, while those at NPB ranged from −23° to −11.8°C.

*Activity*

Adults were usually the first to emerge in the morning and the last to immerge at night. In midsummer at MM, adults usually emerged about 0630 hours. Yearlings emerged about 0700, and young about 0800. Young usually immerged by 1930, yearlings by 1945, and adults between 2000 and 2030. All animals immerged by dark. Emergence and immergence times shifted seasonally with sunrise and sunset. By September, animals did not emerge until 0900 and usually immerged by 1930.

Foraging activity of adults and yearlings at MM peaked in early to mid-morning and again in late afternoon on clear days (Armitage 1962; fig. 3). Foraging activity of young was more uniformly distributed during the day. Foraging activity of a female at PIC during a week of cloudy weather and lower $T_{es}$'s was also more uniformly distributed (fig. 4). Young at NPB spent more time foraging during midday than did young at MM (see, e.g., fig. 5) and also spent more total time foraging—an average of 6.0 h $d^{-1}$ during a 3-

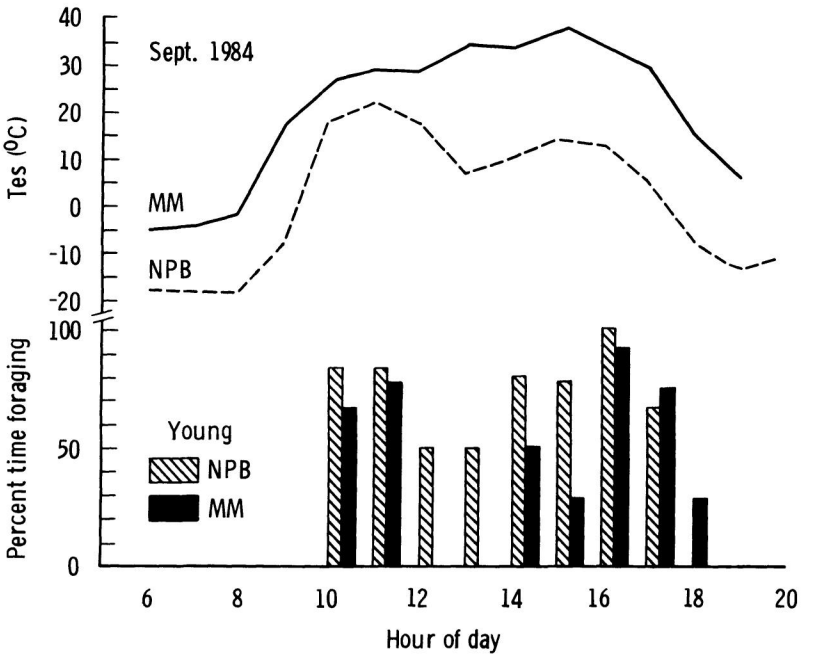


*Fig. 5. Foraging activity (percentage of time spent foraging) and* $T_{es}$*'s averaged over hourly intervals for young at Marmot Meadow and North Pole Basin during a 3-d study in September.*

d study in September compared to 4.3 h $d^{-1}$ for young at MM during the same period. No simultaneous comparisons were available for adults, but two females at NPB spent an average of 6.8 h $d^{-1}$ foraging during a 3-d study in August compared to an average of 3.6 h $d^{-1}$ for three females at MM and PIC during week-long studies in July. Marmots at all study sites shortened foraging bouts at high $T_{es}$'s (fig. 6). There appeared to be a curvilinear boundary effect of $T_{es}$ on maximum foraging-bout length. As $T_{es}$ increased, maximum foraging-bout length decreased hyperbolically. This relationship suggested that the outer limits of foraging-bout length were set by $T_{es}$ (at least at stressful $T_{es}$'s) and foraging-bout length within the boundary was determined by other factors. Marmots active above ground for extended periods at high $T_{es}$'s alternated foraging with sitting on rocks, where higher wind speeds produced lower $T_{es}$'s (e.g., activity records of marmots given in fig. 7). Although marmots were active at $T_{es}$'s above thermal neutrality, adults made little use of the time available at the high $T_{es}$'s (fig. 8). By contrast, young used relatively more of the high $T_{es}$ time, and adults used relatively more of the low $T_{es}$ time. At NPB, where high $T_{es}$ time was unavailable, young used most of the time available at moderate $T_{es}$'s (5°–24°, fig. 8). At MM, young mostly avoided the low $T_{es}$'s at which the NPB young were active.

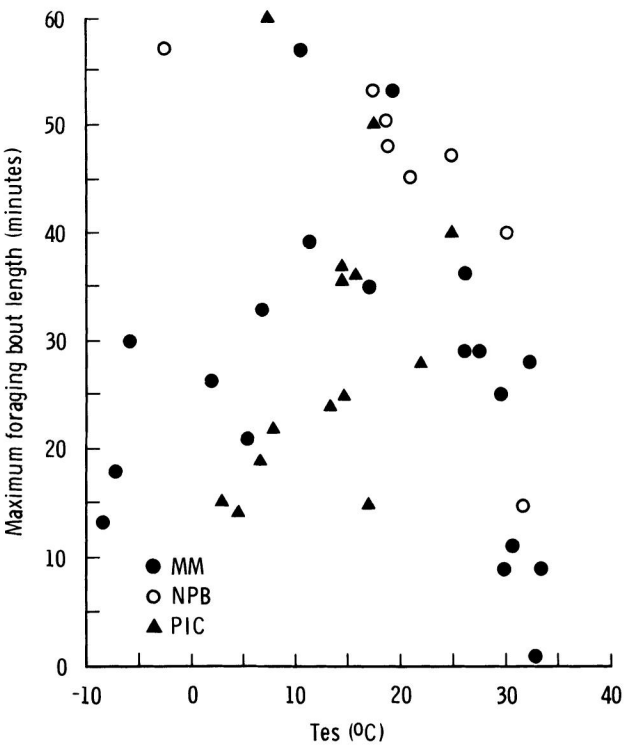


*Fig. 6. Maximum foraging-bout length recorded during each hourly interval in which an animal was active plotted against average* $T_{es}$ *for that hour, for female 911 at Marmot Meadow during a mostly clear week in July, female 573 at Picnic during a mostly cloudy week in July, and for two females at North Pole Basin during a mostly clear 3-d period in August.*

*Body Temperature*

The daily range of $T_b$ was similar for all animals, from nighttime lows averaging 36.6°C to daytime highs averaging 39.8°C (Melcher 1987). Marmots' $T_b$'s generally rose before they left their burrows in the morning; their $T_b$'s above ground varied with activity (fig. 7). Values for $T_b$ usually rose while marmots were foraging, at rates up to 0.075°C $min^{-1}$ for adults and 0.114°C $min^{-1}$ for young. The $T_b$'s of active animals rarely exceeded 40°C; marmots usually ceased foraging and either perched on rocks or entered their burrows when $T_b$ neared 40°C (fig. 7).

## Discussion

Thermal conditions in yellow-bellied marmot habitats include times of heat stress as well as times of cold stress. Thermal stress can limit time available

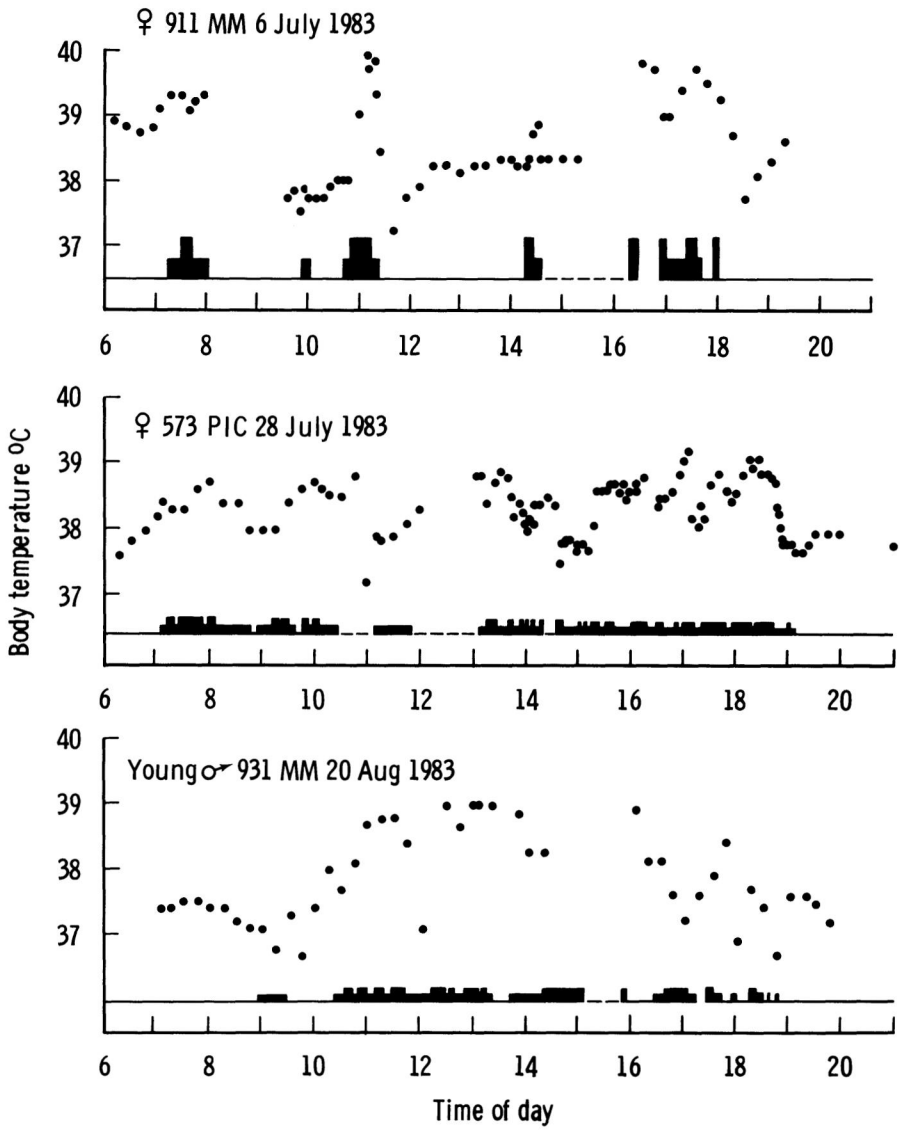


*Fig. 7. Body temperature and activity of individual marmots. Symbols plotted beneath body temperatures indicate activity: solid horizontal line indicates animal in burrow; broken horizontal line indicates animal's location uncertain; lower vertical bar indicates animal sitting on rocks above ground; and higher vertical bar indicates animal foraging.*

for foraging or increase foraging costs by requiring thermoregulatory energy expenditure. Because marmots have only a short active season, fitness should be greater for individuals that time activity to maximize use of available foraging time and minimize thermoregulatory costs.

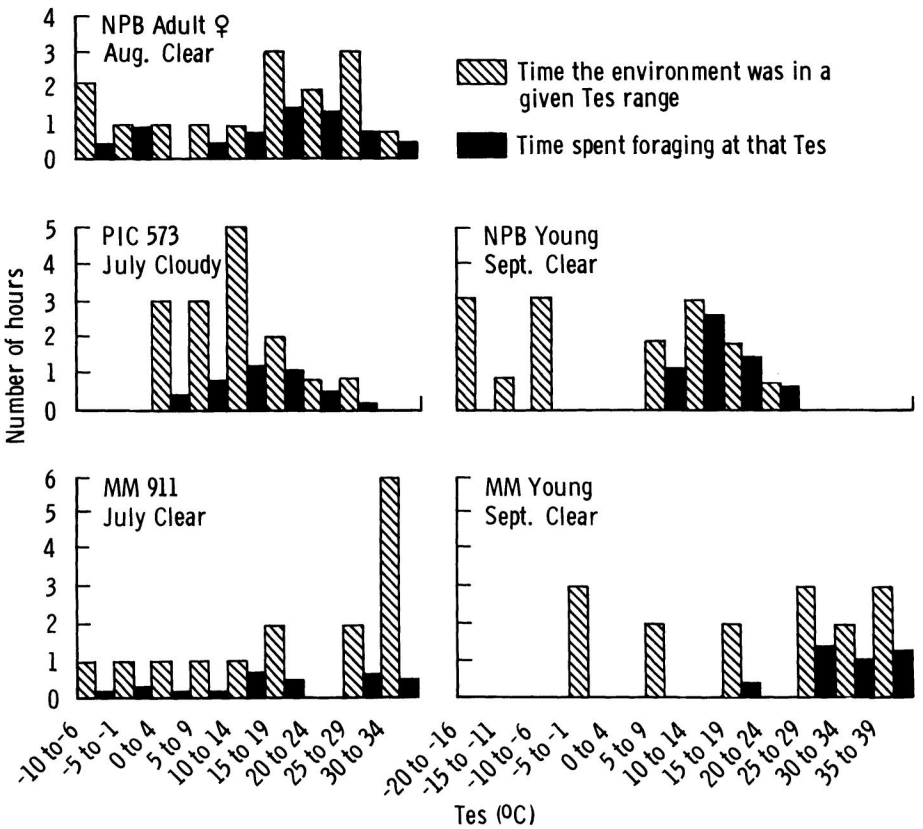


*Fig. 8. Distribution of* $T_{es}$*'s and foraging activity for marmots and study periods noted in figs. 5 and 6. Within each range of* $T_{es}$*, the amount of time the environment was in that range and the amount of time spent foraging are presented as daily averages. Animals 573 and 911 were adult females.*

*Thermal Influences on Activity*

The $T_{es}$'s for adults and yearlings in foraging areas at MM and PIC often exceeded 30°C between 1100 and 1600 hours on clear days, and $T_{es}$'s for young often exceeded 25°C during those hours (see, e.g., fig. 1). Marmots are not well adapted physiologically to cope with high heat loads and became severely heat stressed at $T_a$'s above 20°C during laboratory measurements of oxygen consumption (Ward 1980). Marmots in the field responded to high $T_{es}$'s in part by reducing foraging activity (fig. 3). Webb (1980) also observed that young foraged less at high $T_{es}$'s.

Marmots foraging during the hottest hours on clear days had few options for avoiding heat stress. Shade was usually unavailable in foraging areas. Marmots foraged at high $T_{es}$'s mainly by tolerating transient increases in $T_b$

but reduced foraging-bout length to avoid $T_b$'s over 40 °C (fig. 6). The antelope ground squirrel similarly shortens activity bouts at high $T_{es}$'s (Chappell and Bartholomew 1981*b*). Marmots active above ground for extended periods at high $T_{es}$'s typically alternated foraging with sitting on rocks (fig. 7) where higher wind speeds reduced $T_{es}$'s by up to 10 °C. Heller and Gates (1971) reported similar behavior for alpine chipmunks (*Eutamias alpinus*) active at midday. Perching on rocks rather than retreating to the burrow to dissipate stored heat may have facilitated predator surveillance between foraging bouts or served a social function.

Marmots, particularly young, faced high thermoregulatory demands if they were active above ground during the coldest daylight hours. The $T_{es}$'s for all age classes were often below zero before 0800 hours. Oxygen consumption of marmots has not been measured at $T_a$'s below 5 °C, but oxygen consumption at 5 °C was about twice that in the thermoneutral zone (TNZ) (Kilgore and Armitage 1978; Melcher 1987; Armitage, Melcher, and Ward 1990). Young contended with cold stress mainly by avoidance, delaying emergence until after 0800 hours and immerging before $T_{es}$ fell to stressful levels in the evening (figs. 3 and 8). Young sometimes foraged at low $T_{es}$'s, however; young at NPB were active on a heavily overcast September day on which $T_{es}$ never rose above 0 °C. Young may routinely avoid aboveground activity at low $T_{es}$ when possible but forage at low $T_{es}$ if such activity is necessary to meet daily energy needs and preferable to the alternative of forgoing foraging.

Marmots generally responded to stressful $T_{es}$'s by reducing foraging activity to avoid heat stress at high $T_{es}$'s and high thermoregulatory costs at low $T_{es}$'s. Although marmots reduced thermoregulatory costs by avoiding most low $T_{es}$'s, they sometimes foraged at stressful $T_{es}$'s while not making full use of all available time at more moderate $T_{es}$'s (fig. 8). Some time at moderate $T_{es}$'s may not have been used for foraging because animals had eaten to satiation during prior foraging bouts and needed time to digest food, because time was needed for other activities, and perhaps because of social interactions (discussed below). Time available for foraging probably exceeded time needed for foraging except under limited circumstances. Young seem most likely to have experienced a combination of high energy demands, decreasing availability and quality of vegetation, and high $T_{es}$'s that limited time needed for foraging.

Midday $T_{es}$'s at MM during September 1984 were among the highest recorded; time available for aboveground activity was reduced because of seasonal reduction in number of daylight hours; and nitrogen and water content of food was decreasing (Frase and Armitage 1989). Under these conditions high $T_{es}$'s may have limited foraging time needed to meet energy demands.

Energy intake of a young male was insufficient to meet daily energy expenditure during the time of the study (Melcher, Armitage, and Porter 1989). This animal probably did not reach the threshold weight needed to survive hibernation, for it did not survive the winter.

*Thermal Influences and Energetics*

Ideally, a study of thermal influences on available foraging time and thermoregulatory costs incurred while foraging would evaluate their importance in terms of effects on fitness-related factors such as growth or fat deposition rates (Kingsolver 1983; Tracy and Christian 1986). We estimated that thermoregulatory costs of alternative activity schedules that involved foraging at the coldest daylight $T_{es}$'s would be two to five times greater than actual daily thermoregulatory costs (Melcher et al. 1989) required by the alternative schedules. Additional thermoregulatory expenditure represented 12% of the energy allocated to growth by a young male at NPB and 18% of the energy allocated to fat deposition by a female at MM. However, uncertainties regarding the energetic costs of different activities at different $T_{es}$'s and the difficulty of modeling transient changes in $T_b$ and activity in thermally heterogeneous environments make attempts to translate thermal influences into terms relevant to growth or fat deposition problematic. Given the limits of the data in this study, it is more appropriate to simply suggest some relationships between thermal influences and marmot ecology.

Growth rates of young at NPB are higher than those of young at MM and PIC (Andersen et al. 1976); lower $T_{es}$'s at NPB may enable animals to spend more time foraging—hence the higher growth rates. Young at NPB in September spent more time foraging than young at MM and also foraged during midday hours when young at MM did not (fig. 5). Webb (1980) found that high $T_{es}$'s limited available foraging time more at low than at high elevations. Estimation of the contribution of differences in available foraging time to differences in growth rate is complicated by differences in vegetation between the two sites. The nitrogen and water content of vegetation at MM in late summer was less than that of vegetation at NPB (Melcher et al. 1989); both reduced food quality and reduced available foraging time are likely to have contributed to reduced growth rates at MM.

Thermal conditions may also define, in part, opportunities for social interaction or avoidance. Most marmots disperse as yearlings. The timing of dispersal of males is directly related to amicable behavior; when rates of amicable interactions were high, yearling males remained longer at a site (Downhower and Armitage 1981). Large males tended to disperse earlier; female yearlings dispersed early when rates of aggression were high. Year-

lings emerge from hibernation weighing less than 1 kg but grow rapidly to more than 2 kg by midsummer. The $T_{es}$'s for yearlings then become similar to those for adults and impose similar thermal constraints on activity. Thus, yearlings have less opportunity to avoid agonistic behavior by selecting an activity schedule different from that of adults and may be forced to disperse to escape social harassment. Social behavior among adult females, especially those more distantly related than sisters or mother and daughters, is characterized by agonistic behavior (Armitage 1986), and subordinate animals often are forced to move to inferior habitat. These moves may be necessary because adult females have restricted options for modifying their daily activity to avoid encounters with a dominant animal. Because the dominant animal is active during energetically favorable times, the subordinate animal would be forced into activity bouts at more thermally stressful times. It thus seems likely that the thermal environment imposes constraints on the response of marmots to the social environment.

## Acknowledgments

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